J. New York Entomol. Soc. 101(4):515–530, 1993

THE MORPHOLOGY, NATURAL HISTORY, AND BEHAVIOR OF THE EARLY STAGES OF *MORPHO CYPRIS* (NYMPHALIDAE: MORPHINAE)—140 YEARS AFTER FORMAL RECOGNITION OF THE BUTTERFLY

P. J. DeVries[1] and George Eujens Martinez[2]

[1]Museum of Comparative Zoology, Harvard University,
Cambridge, Massachusetts 02138; and
[2]Department of Entomology, American Museum of Natural History,
Central Park West at 79th St., New York, New York 10024

Abstract.—The morphology, natural history and behavior of *Morpho cypris* immature stages are described for the first time. The location and use of two secretory glands, one that was previously undescribed, are noted and discussed with respect to glands found in other groups of Lepidoptera. A comparison of *Morpho cypris* early stage development, behavior, defenses, and host plant use within the context of the genus *Morpho,* and the subfamily Morphinae is provided.

A survey to elect a butterfly that exemplifies the neotropics would very likely result in most ballots being cast for the genus *Morpho*—one of the most conspicuous of all butterflies. Historically these butterflies have captured the imagination of visitors to the neotropics; testimonies to this are found in accounts of the early naturalists (e.g., Bates, 1864; Belt, 1874). Today frequent references to *Morpho* are found in travel brochures and natural history articles, and they are often centerpieces for the popular butterfly houses. No one can fail to be impressed by the sight of *Morpho* butterflies because, alive or dead, they delight the imagination, and give pause for thought.

A literature inspired mainly by collectors and insect dealers treats *Morpho* butterflies as art objects. In this system the collectors want their cabinets filled with as many named specimens as possible, and it is to the advantage of dealers to offer a variety of units for sale. The collectors/dealers interested in *Morpho* found that many of the species are wide ranging and variable, and thus fertile ground for the naming of forms, aberrations, and even individual specimens. For example, the magnum opus written by the enthusiastic dealer and collector Eugene Le Moult recognizes over 70 species, and hundreds of forms of *Morpho*—at least 77 forms of which he described himself (Le Moult and Real, 1962). Perhaps the proliferation of names was good for business, but to the serious student of butterflies it was excessive. In his overview of the neotropical fauna, D'Abrera soberly recognizes 27 species of *Morpho,* and points out that Le Moult and Real's work is more of a commercial catalogue than a serious taxonomic revision (D'Abrera, 1984).

Although there is a substantial anecdotal literature, relatively little work has been published on the early stages or life cycles of *Morpho.* The work of A. Young and his colleagues has furthered our understanding of the Central American species (see Young, 1982 and included citations), while Otero (1966) has summarized natural history information on some of the South American species. Two broader systematic works that provide information relevant to *Morpho* early stages include a summary of host plant associations (Ackery, 1988) and morphological details of caterpillars in the Morphinae (DeVries et al., 1985). However, despite their historical popularity and obvious presence in lowland tropical habitats, the early stages of most *Morpho* species remain unknown.

Morpho cypris Westwood, 1851, ranges from Nicaragua to Colombia and Venezuela occurring in rain forest habitats from sea level to about 700 m elevation. The males of *M. cypris* possess a brilliant blue structural coloration on the dorsal surface, whereas the female may either be yellowish on the dorsal surface, or have a blue coloration similar to the males. Both sexes typically utilize thermal upwellings along rivers and streams to 'float' high in the forest canopy, and thus largely elude observation or capture. The coloration and elusive habits of *M. cypris* have made it one of the most sought after butterflies in the world. Nevertheless, our understanding of the early stages of this spectacular species is confined to a few illustrations and notes (DeVries, 1987). The goals of this paper are to provide a more detailed account of early stage morphology and behavior of *M. cypris,* as well as briefly to compare our findings to other studies of *Morpho* immatures. After more than 140 years since its original description we hope that the rudimentary biology of *M. cypris* will assist students of natural history and conservation biology: 140 years into the future, there may be nothing left of these organisms and their habitats to understand.

MATERIALS AND METHODS

Observations were made on *Morpho cypris* by DeVries from 1 July to 12 November 1984 at the Sirena station, Parque Nacional Corcovado, Costa Rica located on the Pacific coast. The surrounding forest types at Sirena include: lowland primary rain forest, degraded primary forest, flood plain forest, mangrove forest, second-growth forest that has regenerated after being clear-cut, and maintained pasture. Early instars were kept in small plastic containers with tight fitting lids, and as the caterpillars matured, they were kept in plastic bags that were cleaned twice daily. All observations and rearings were done in the field at ambient temperatures. Adults, immatures, and behaviors were photographed by DeVries, and these photos were later used for drawings by Martinez. Terminology of immature morphology and chaetotaxy follows Peterson (1962) and Stehr (1987). Representative early stage material was preserved in alcohol, and these specimens, along with cast skins and adult vouchers are deposited in the collection of DeVries, and in The Natural History Museum, London. Voucher material of the host plant was deposited in the herbarium of the Museo Nacional de Costa Rica.

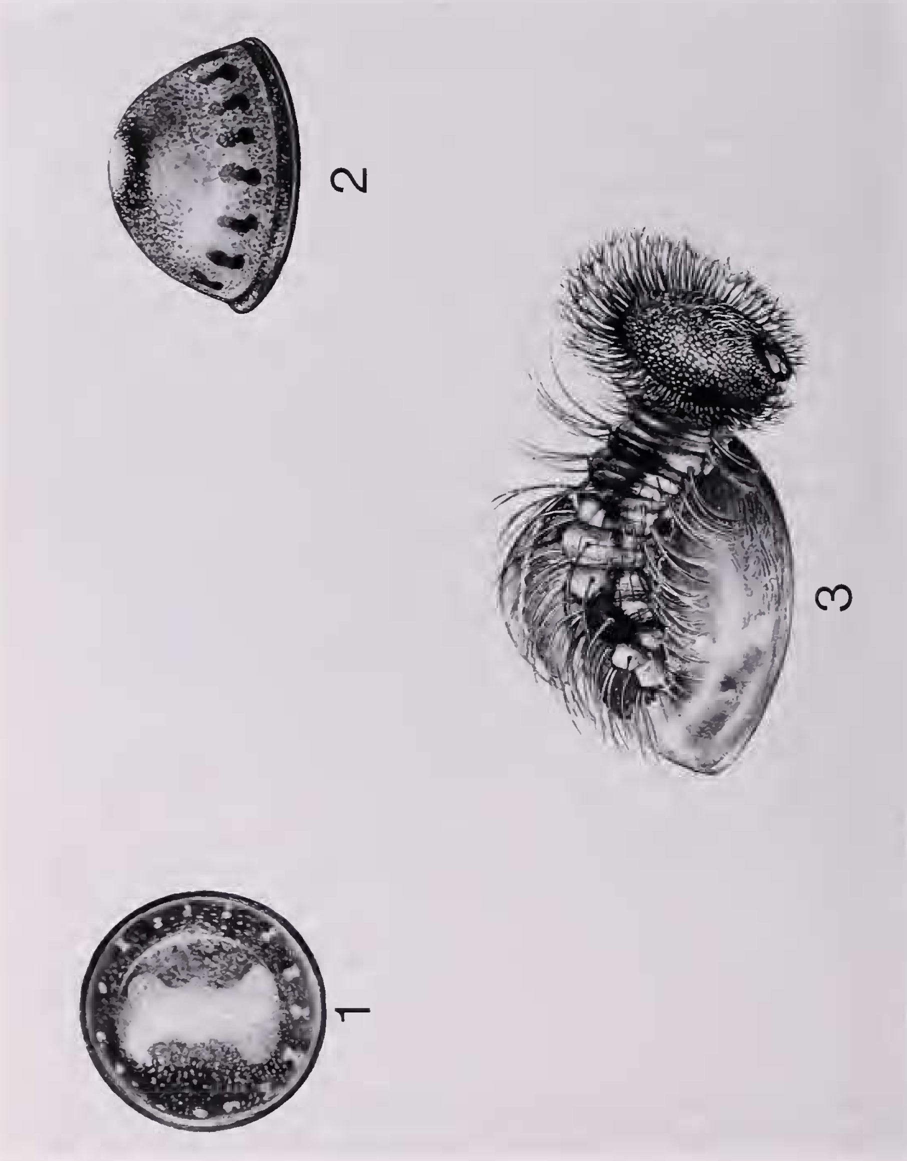
RESULTS

Oviposition behavior: Between 09:55 and 10:05 hours on 1 July 1984 PJD observed a female *M. cypris* (yellow form) oviposit at least 14 eggs on the leaves of a large, isolated *Inga marginata* (Fabaceae) tree that was growing in a pasture used to maintain horses. The tree was located about 25 m from the forest edge, and had a full, rounded canopy that presumably was the result of having grown in the open for at least five years. Within a few seconds after landing on the foliage, the female deposited a single egg on the dorsal surface of a leaflet, then immediately took flight, circled the tree, landed, and repeated oviposition. There were generally 10–20 second intervals between egg depositions, and oviposition sites ranged from leaves located on the inside of the tree crown within 1.5 m of the ground to leaves 15 m above the ground on the outside of the crown. All ovipositions took place in direct, bright sunshine. The female flew about and landed on the foliage in a haphazard fashion, exhibiting none of the inspection behavior prior to oviposition seen in other butterflies, such as *Parides* or *Heliconius* (see DeVries 1987). Presumably, the rapid, haphazard oviposition behavior in *M. cypris* reflects two related traits: 1) flight speed and agility are affected by an abdomen heavily loaded with eggs, and 2) *Morpho* butterflies are palatable to vertebrate predators (Chai, 1990). When PJD later climbed the tree he was able to find only 2 of the 14 oviposition sites, despite over an hour of careful searching. The eggs are extremely cryptic, and appear similar to small galls that occurred on many of the *I. marginata* leaves.

At 10:05 the fresh, undamaged female (wing length = 80.5 mm) was captured and confined with cuttings of the host plant in a 4 × 4 m screened cage. Between 2–4 July she was induced to oviposit under artificial conditions. After being fed on fruit juices, she was held by the fore wings, allowed to flutter the hind wings, and then placed on an *I. marginata* leaf. Upon contact she typically 'tasted the leaf' by rapidly and audibly drumming on the leaf surface with the forelegs. After drumming she brought her abdomen in contact with the leaf surface, pressed the characteristic Morphinae papillae anales (see DeVries et al., 1985) tightly to the leaf surface, opened them, and usually deposited a single egg (although treated in this manner she occasionally laid 5–7 eggs sequentially). This process was repeated intermittently until the female became fatigued and refused to oviposit.

The total egg output during induced oviposition was 36 eggs on 2 July, 18 eggs on 3 July, and 5 on 4 July, yielding a total of 59 eggs, 57 of which were fertile. The female died from injuries sustained from *Solenopsis* sp. (Myrmecinae) ants that attacked her during the evening of 4 July. She weighed 1.7 grams the morning of 5 July, and an autopsy revealed 9 almost completely developed eggs plus whitish-yellow lipids in her abdomen. Had she lived, presumably this female would have continued to produce more eggs.

Egg: (Figs. 1–3)—Hemispherical, smooth, with no visible sculpturing, but with a rounded rim where base contacts leaf surface. When laid the entire egg is pale translucent yellow-green, and without markings. Within 24 hours the egg appears to contain a milky, bone shape (presumably the embryonic larva) suspended in the center (when viewed dorsally), and in lateral view there is a broken, milky row of short, irregular, vertically oriented peanut-shapes that encircle the egg slightly above the base. Within 38 hours the egg becomes semi-translucent and golden-green, the peanut-shapes turn crimson, and the dome bears a crimson circle surrounding a whitish micropyle. Nine days after being laid the chorion becomes transparent, and the red head of the larva can be seen easily at the dome of the egg (including the mandibles and stemmata), surrounded by the red and white patches of the body that is coiled around the lateral edges of the egg. Close inspection at this phase reveals that the egg contains a fluid, and a well defined air pocket between the base of the head and the body. Between 10 and 11 days after being laid the caterpillar cuts through the chorion, extrudes the mandibles, cuts the dome away in a circular fashion, then exits the egg (Fig. 3). Upon exiting the egg, first instars typically ate all of the



Figs. 1–3. Egg and hatching first instar caterpillar of *Morpho cypris.* 1. Dorsal view of egg. 2. Lateral view of egg. 3. First instar emerging from the egg.

chorion excepting the opercular dome and the base, performed a grooming behavior (see below), and did not feed for 24 hours.

First instar: (Fig. 4) *Head*—deep maroon; frons convex without setae, but bearing many pits and surface granulations; area above the frontoclypeus with a tuft of short, maroon setae that project forward; outside perimeter of head capsule with a prominent, dense corona of long, maroon setae that almost encircle head, excepting near mandibular area where setae are shorter; coronal setae curved forward and forked distally into 3–4 finer filaments; head much wider than body. *Body*—pale cream-yellow with three conspicuous, reddish-maroon rectangular patterns on dorsum, each with six filamentous arms (three per side) which extend dorsally, then downward along lateral portion of body; first maroon pattern extends from T-1 to A-1, second from A-4 to A-5 (leaving a yellow spot that will become one of two ovals in later instars), and last maroon pattern extends from A-7 to A-8; all subdorsal and lateral setae bear spurs along shafts and arise from pinaculae; abdominal setae blonde and curved to posterior; setae on T-1 and T-2 maroon-red, curve to anterior, and flow into corona of head setae; anal plate terminates in a distinct cream-yellow bifid tail.

Caterpillars fed at the leaf edges, producing deep, irregular-edged sinuses. Typically a caterpillar began at an undamaged portion of a leaf each time it began a feeding bout. The caterpillars fed intermittently during 24 hour periods, and rested on the host plant leaves. Premolt duration from first to second instar = 24 hours. Total first instar duration 17.7 days (N = 20, SE = 0.424).

Second instar: (Fig. 5) *Head*—deep maroon, wider than body; frons with a sparse covering of setae interspersed with surface pits and granulations; ecdysial lines and mandibular area with short, downy white setae; maroon coronal setae denser, more robust, and interspersed with stiff, darker maroon (almost black) setae along perimeter of head; all coronal setae are distally plumose and curved forward. *Body*—bright, chrome yellow with the three dorsal, rectangular patterns very dark maroon (almost black); pattern on T-1 to A-1 has narrowed considerably, with its posterior arms fusing with anterior arms of pattern on A-4 to A-5 to embrace a yellow oval; center of maroon pattern on A-5 bears two dense tufts of crimson subdorsal setae that curve to posterior, and these tufts persist in all subsequent instars; posterior arms of dorsal rectangular pattern on A-4 to A-5 almost join anterior arms of pattern on A-7 to A-8, and begin to define a yellow oval; all setae are denser and more obviously spurred on shafts; lateral setae now within tufts of long and short setae; subdorsal setae on T-1 and T-2 obviously spurred, flow into coronal setae, and now pale maroon to blonde; bifid tail on A-10 red with short translucent setae.

Feeding behavior was similar to that described for first instars. Caterpillars fed intermittently during 24 hour periods, and rested on the host plant leaves. Premolt duration from second to third instar = 24–36 hours. Total second instar duration 16.9 days (N = 13, SE = 0.265).

Third instar: (Fig. 6) *Head*—similar to second instar, wider than body but slightly more proportionate and more evenly covered with maroon and black setae; setae along the ecdysial lines now gray, and include wider lines of gray setae on either side of ecdysial lines. *Body*—yellow with a tinge of green; arms of dark maroon patterns are prominent and fused, defining the two dorsal ovals; red bifid tail on A-10 slightly more prominent.

Feeding behavior now included removing most of one side of an *Inga marginata* leaflet, leaving a few irregular lobes near the mid-vein. Caterpillars fed intermittently throughout 24 hour periods, and rested on the host plant leaves. Premolt duration from third to fourth instar = 36 to 48 hours. Total third instar duration 19.3 days (N = 9, SE = 0.33).

Fourth instar: (Fig. 7) *Head*—similar to third instar, but slightly wider than body, with setae covering the entire head; setae longest along perimeter of head, shorter on frons, and shortest near mandibles; gray setae along ecdysial lines, and on either side wider, more diffuse, and generally more conspicuous, especially on frons. *Body*—overall color now distinctly yellow-green (especially dorsal ovals); dark maroon patterns inset with fine filigree cream and pale maroon patterns; A-1 with two tufts of short, erect subdorsal setae that define the location of grooming gland (see below); subdorsal setal tufts on A-5 are now bicolored, composed of longer white anterior setae, and shorter red posterior setae; posterior edge of maroon pattern on A-5 now contains a small, roundly triangular, yellow-green spot (that will persist in subsequent instar) which weakly joins posterior oval; A-8 now with two small, subdorsal tufts of setae that curve to posterior and colored as in tufts on A-5; bifid tail on A-10 now deep maroon with reddish setae.

Feeding behavior was similar to that described for third instars, except the caterpillar can now devour an entire leaflet. Feeding typically occurred at dawn and dusk, but caterpillars occasionally fed during the day. This instar remained on the host plant leaves when not feeding. Premolt duration from fourth to fifth instar = 36 to 48 hours. Total fourth instar duration 35.7 days (N = 7; SE = 0.286).

Fifth instar, first color phase: (Fig. 8) *Head*—slightly wider than body; dominant coronal setae gray interspersed with reddish-brown, all setae of uniform length; setae along ecdysial lines and frons white, shorter and denser than coronal setae. *Body*—overall a deep banana yellow, without green overcast as in previous instars; dorsal patterns dark red-brown, completely framing two ovals, and extensively marbled with cream-colored filigree; center of each oval bearing a barely discernible filigree of two elongate, jagged rectangles separated by dorsal line; in addition to subdorsal tufts on A-1 and A-5, now A-2 with subdorsal tufts straddling the anterior section of anterior oval, A-4 with pair of subdorsal tufts that straddle posterior section of anterior oval, A-7 with pair of subdorsal tufts that straddle posterior section of posterior oval, and A-8 with a pair of subdorsal tufts; these four pairs of newly developed subdorsal tufts are short, maroon-red in center with some white on anterior portion, and curved to posterior; longest subdorsal setae are denser, obviously spurred, and curve to posterior; lateral setae are blonde to white, obviously spurred, and completely obscure legs; subdorsal setae on T-1 and T-2 flowing into corona now maroon and gray; bifid tail on A-10 deep maroon with maroon setae.

After molting to the fifth instar the caterpillar began to steadily lose its deep yellow color, and became more and more cryptic. Between days six and eight of this instar the caterpillar completed its extraordinary change in appearance.

Fifth instar, second color phase: (Fig. 9) *Head*—same width as body; dominant coronal setae grayer than previously; head capsule itself faded to red-brown, showing only a blush of maroon. *Body*—overall coloration gives the impression of yellowed and grizzled antique ivory covered with an overlay of the fine scrimshaw, including both dorsal ovals which are filled with a complex pattern of black elongate rectangles and tiny brown dots. Excepting bifid tail on A-10 (which remains red), all bright yellow, red, and maroon body coloration has been lost. Even more remarkable is that, excepting the maroon subdorsal tufts on A-1, the other five pairs of subdorsal tufts have mostly faded to white, retaining only central maroon setae. The overall appearance of the caterpillar now suggests a dry twig of gray wood.

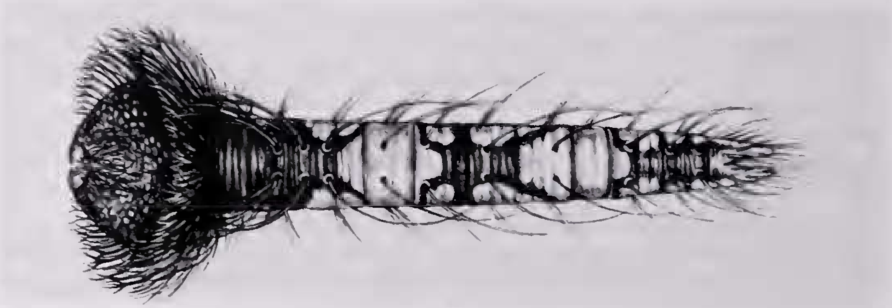
In both color phases the fifth instar caterpillars exhibited feeding behavior similar to the fourth instars. However, fifth instars fed nocturnally, only between dawn and dusk, and rested off the host plant. Premolt duration from fifth star to pupa = 3 to 4 days. Total fifth instar duration 30.3 days (N = 3, SE = 0.66).

Secretory glands: The caterpillars of *M. cypris* possess at least two secretory glands, both likely to serve a defensive function. The cervical gland, which occurs on caterpillars of Hesperiidae, Pieridae, Nymphalidae, and Notodontidae (Bourgone, 1951; Peterson, 1962; Miller, 1991), secretes a volatile chemical when a caterpillar is molested. The other gland, which has apparently never been described previously, secretes a liquid that is groomed into the subdorsal tufts of setae. Studies describing the morphology of these glands are currently in progress, and will be reported elsewhere (DeVries and Shinn, in prep.).

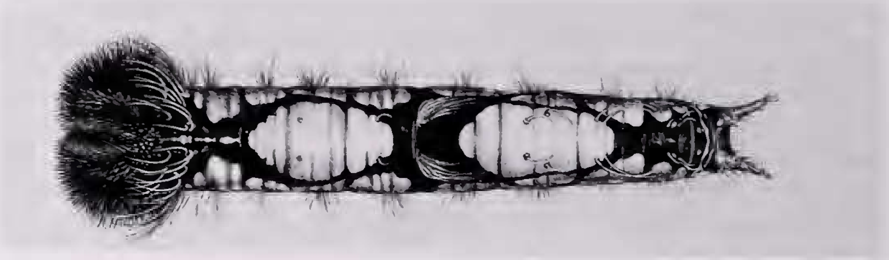
The cervical gland: When a third and later instar was prodded or molested, the caterpillar raised the head such that the mandibles projected forward, and extruded a red, bluntly cylindrical cervical gland from a slit located anterior to the first set of legs. The gland usually remained extruded for about five seconds before being retracted. While extruded it emitted an odor, reminiscent of rotten tomatoes, that lingered for a few seconds after the gland had been retracted. Larger caterpillars produced a stronger odor than did the smaller ones. It has not been determined whether first and second instars possess this gland. Unlike those described for some notodontid caterpillars (Forbes, 1948; Kearby, 1975), the cervical gland of *M. cypris* did not produce a spray or cause a noticeable irritation when the extruded gland was brought into contact with the skin.

The grooming gland: Within an hour after molting all instars vibrated their heads up and down rapidly and shallowly, and produced a drop of clear liquid from a dorsal pore located between the subdorsal tufts on A-1, which we term the 'grooming gland'. The drop of liquid was held suspended at the distal portion of these tufts for a few moments (Fig. 10), then the head arched toward the posterior, and the drop was combed into the subdorsal setae on T-1 and T-2. Then with a slow, rotating motion of the head, the drop was combed into all abdominal subdorsal tufts and the setae on the caudal tails. This action was first performed on one side of the body, then after a moment, repeated on the other side, leaving the setal tufts gleaming with the liquid. After about two minutes exposure to sunlight the liquid evaporated from the subdorsal tufts, and they lost their gleaming appearance. Depending on the individual caterpillar, post-molting combing behavior was repeated from three to five times during the span of 30 minutes. The secretion of liquid from the grooming gland and combing behavior was rarely observed the day after molting. However, it may be a common nocturnal behavior that went undetected during this study.

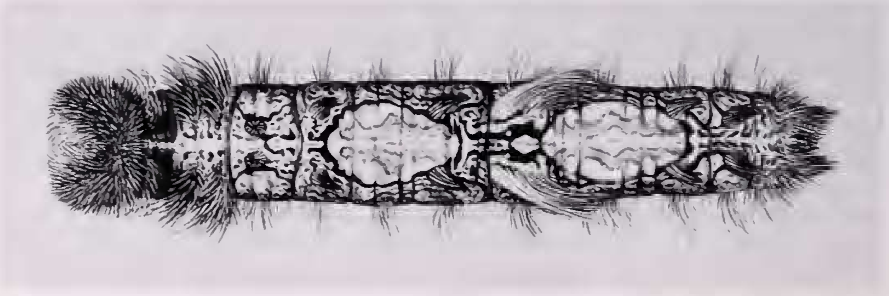
Caterpillar behaviors: Several incidental behaviors are worth noting. First, caterpillars in all instars were observed to eat the dense mat of resting-silk that had been spun prior to molting, and then subsequently eat their cast skin. This behavior took place two to four hours after completing a molt, and always preceded eating leaf tissue. Second, when tickled with a splinter of wood, all instars would violently bring



4

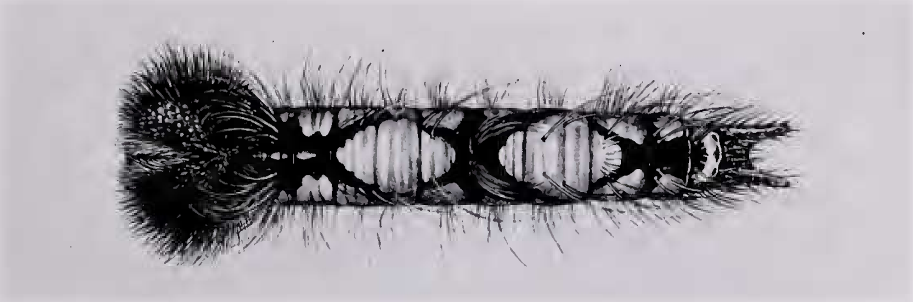


6

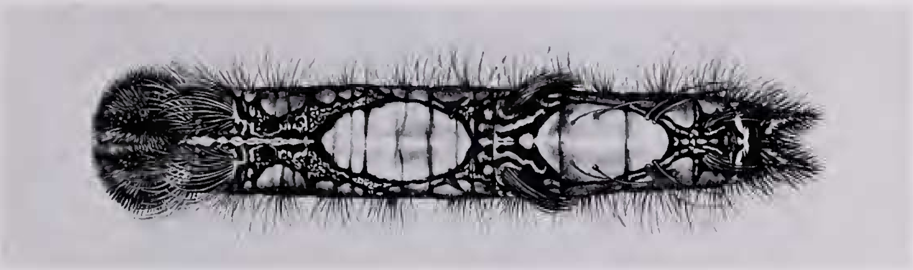


8

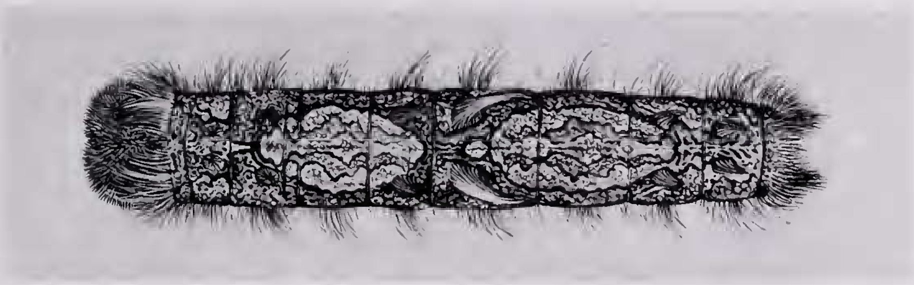
Figs. 4–9. The five caterpillar instars of *Morpho cypris* in dorsal view. 4. First instar. 5. Second instar. 6. Third instar. 7. Fourth instar. 8. Fifth instar (first color phase). 9. Fifth instar



5



7



9

⟵

(second color phase). Note the changes in developmental allometry of the head, subdorsal setae, color pattern, and caudal tails.

their head toward the area of contact, bring the head against the wood, and briskly flicked the head laterally. This action caused the stiff head setae to be used like an 'armed comb' to rebuff the wood away from the body. After being molested in this fashion, various portions of the epidermis slowly twitched, much like a horse trying to rid itself of bothersome flies. At this point the caterpillars were very sensitive to air currents, and the entire body flinched when they were gently blown upon. Finally, when prodded with a finger, third and later instar caterpillars occasionally beat a rapid and audible tattoo on the substrate with their heads. The extrusion of the cervical gland often accompanied the latter two behaviors.

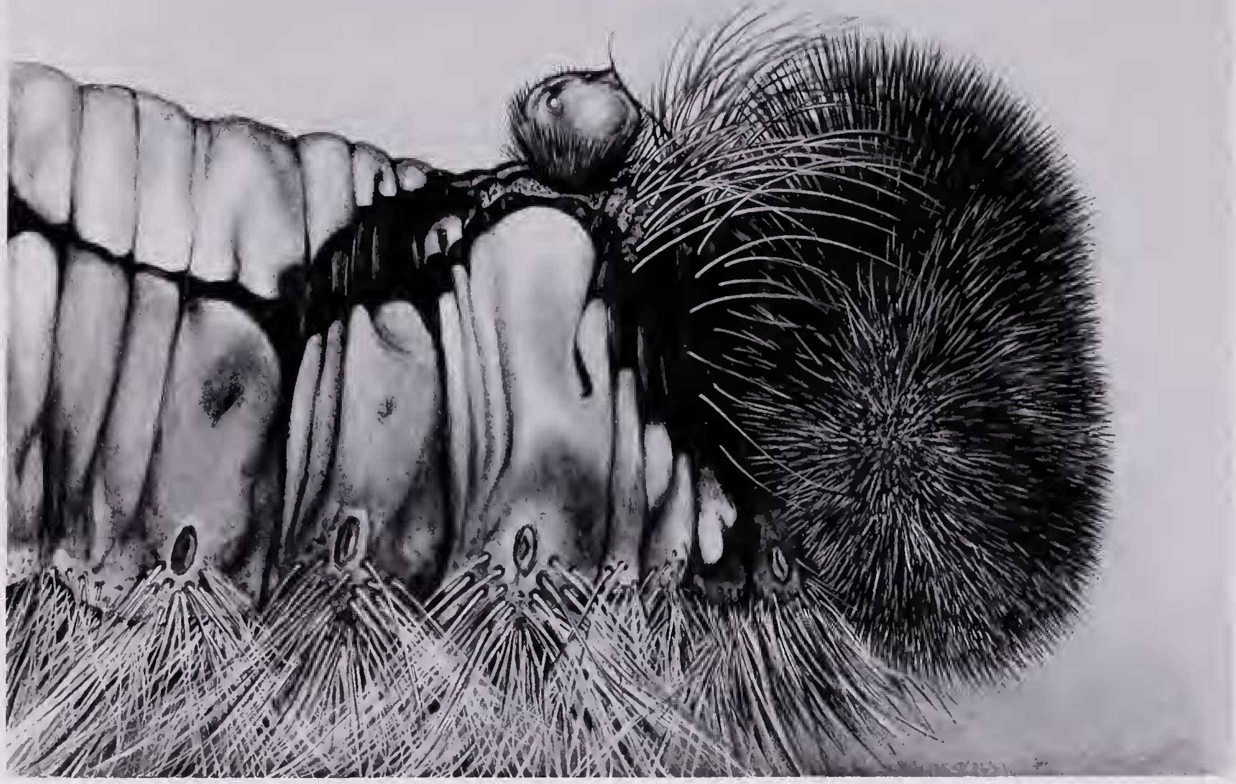
Pupa: (Fig. 11)—Ovoid, with a noticeably globose abdomen widest at A-5, and tapering dramatically toward head; head terminating in a short bifid projection; entire body pale green with a faint whitish bloom, except for yellow spiracles, and a single white ovoid spot covering spiracle on A-5; overall surface smooth except for two minute, brown, rod-like nipples on segment A-10; cremaster brown, granulate, and curved slightly ventrally. When molested the pupa articulated laterally from segments A-5 and A-6, and made an audible "snick" sound each time it moved from side to side. Duration of pupal stage 24 to 25 days (N = 2).

DISCUSSION

In this study 59 viable eggs were recovered from a single, yellow form *M. cypris* through natural and induced oviposition. Of these eggs, all produced first instar caterpillars that were subsequently reared in captivity under field conditions. Three of these first instar caterpillars developed to pupation, but only two of these pupae produced adults. One male, and one yellow form female eclosed (Figs. 12–13); one male pupa died. Based on the two adults that eclosed, the total time duration of egg to adult was 144 days, several weeks longer than the egg to adult times estimated for three other species of *Morpho* (Young and Muyshondt, 1972; Young, 1982). Comparison of our data with that presented for *M. polyphemus* (Young and Muyshondt, 1972) indicates that although duration of the egg stage was the same (11 ± 0.5 days), tenure of all other instars, including the pupal stage, was longer for *M. cypris.*

The vast majority of caterpillars in this study died. One fifth instar died from an undetermined tachinid fly maggot that emerged from the caterpillar (but failed to pupariate). In this instance, a minute tachinid egg laid on the host plant leaf was probably introduced into the rearing container, and fed on by a caterpillar. The death of all other caterpillars typically had its onset immediately prior to or following each molt, at which time a caterpillar would stop moving, void very wet frass, die, and putrefy within 24 hours. Although the exact cause of death is unknown, these symptoms strongly suggest infection from a lethal virus.

The 95% caterpillar mortality observed in this study was similar to the 92% mortality found in *M. polyphemus* when reared under laboratory conditions (Young and Muyshondt, 1972). As noted in that study, laboratory mortality rates probably have little relationship to those occurring under natural conditions. Thus, even though *M. cypris* adults are extremely rare at the Sirena station—less than one sighting per year (P. J. DeVries, P. Chai, independent pers. obs.)—the mortality observed in *M. cypris* is likely an artifact of being kept in captivity. Why such a large fraction of caterpillars



10

Fig. 10. Lateral view of newly molted fourth instar *Morpho cypris* showing the clear drop of fluid secreted from the grooming gland, and suspended between the dorsal tufts.

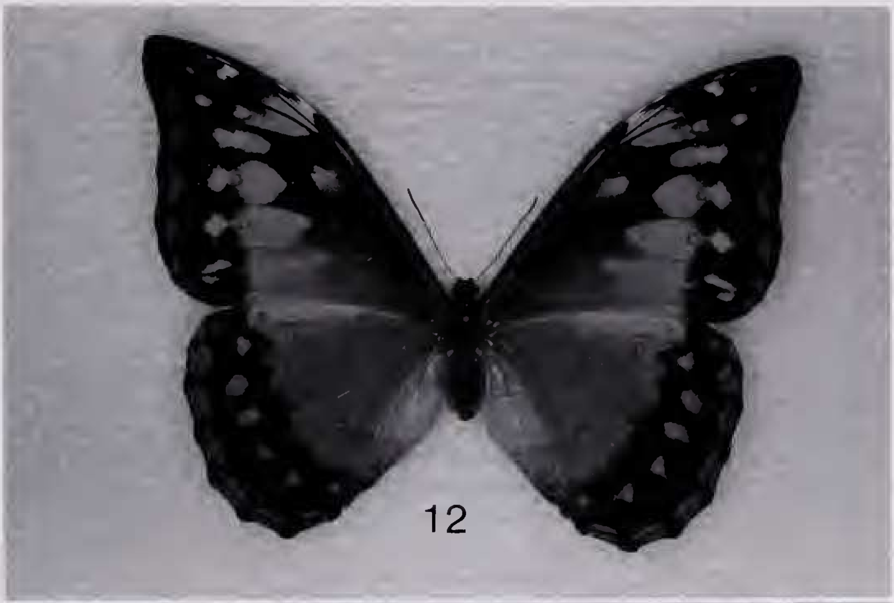
11

Fig. 11. Lateral view of *Morpho cypris* pupa.

died before pupation remains unknown: every attempt was made to ensure that each caterpillar always had access to fresh host plant leaves, and all instars were reared in regularly cleaned individual containers. Such high mortality is in contrast to hundreds of other butterfly species reared by PJD previously, and we feel that if this study had been done under appropriate conditions, whatever those may be, *M. cypris* caterpillar survivorship should have been much higher.

All post–third instar *M. cypris* caterpillars possess a cervical gland that extrudes when a caterpillar is molested. This gland was apparently first noted in caterpillars of *Morpho polyphemus* (Young and Muyshondt, 1972), and has been found subsequently in caterpillars of *Morpho peleides, granadensis, amathonte,* and *theseus* (DeVries, 1987, and unpublished observations). These observations suggest that the cervical gland is a trait shared by all members of the genus *Morpho,* and is at least analogous to cervical glands reported from other groups of Lepidoptera (Bourgone, 1951; Peterson, 1962; Miller, 1991). Within the Nymphalidae the nature of the cervical gland, the conditions when it is extruded, and the odor it emits strongly suggest that it serves as a defense to repel predators. However, we know nothing about the chemistry of this gland for any nymphalid, and have no evidence to indicate what type of predators the gland might repel.

Here we described the dorsal grooming gland found on segment A-1 in all instars of *M. cypris,* and the grooming behavioral response following secretion of a drop of liquid (Fig. 10). The liquid anointed onto the subdorsal tufts may have some defensive function, perhaps serving to repel ants or parasitoids in some way, but we have no observations to support this notion. Six species of *Morpho* caterpillars (*cypris, peleides, granadensis, amathonte, theseus, deidamia*) are known to have a dorsal groom-



12

13

Figs. 12–13. Female *Morpho cypris* that emerged from a pupa resulting from this study (Forewing length = 70.0 mm). 12. dorsal view. 13. ventral view.

ing gland and to show grooming behavior (DeVries, 1987, and unpublished), which suggests that these glands too are widespread within the genus *Morpho.* However, additional *Morpho* species and other genera (e.g., *Antirrhea, Caerois*) should be examined to determine how widely these traits occur within the Morphinae. Our observations suggest that caterpillars in other groups of Lepidoptera that possess setal tufts (e.g., Amathusiinae, Arctiidae, Apatelodidae, Noctuidae, Lymantriidae) should be examined for the presence of similar grooming glands.

Fourth and fifth instar *M. cypris* caterpillars may possess two potential defenses that are directed at vertebrate predators. First, when prodded with a splinter of wood the caterpillars contract their bodies such that the dorsal tufts of setae expand and expose the concealed red-maroon setae. Although none of these setae caused discomfort when brought into contact with the inner arm (DeVries, pers. obs.), the behavior is similar to some tropical lymantriid and megalopygid moth caterpillars that possess urticating, often colored spines buried in setal tufts that are exposed when the caterpillars are molested (DeVries, pers. obs.). Secondly, when molested the *M. cypris* caterpillars bring their heads violently into contact with the stimulus. Some of the head setae are stiff enough to enter the soft skin between the fingers if pushed hard enough, much like a tiny plant spine (DeVries, pers. obs.). However, when embedded into the skin and thrummed with another finger the spines do not produce a chemical burning sensation. The behavior of exposing the red-maroon setae, and the possession of stiff head setae, suggest that *M. cypris* caterpillars may mimic caterpillar species whose urticating spines and warning coloration deter vertebrate predators, like monkeys (DeVries, pers. obs.).

The host plant of *M. cypris* reported here (*Inga marginata*) is a widespread, medium-sized tree that occurs in lowland to montane rain forest habitats ranging from Costa Rica to Brazil—a distribution overlapping that of *M. cypris.* However, several observations suggest that *M. cypris* caterpillars may feed on other plant species as well. During June 1989 at about 14:00 hr DeVries observed a *M. cypris* female ovipositing high in the canopy of several large *Inga* trees growing inside the forest at Rara Avis (El Plastico, Heredia Province, 750 m, Atlantic slope of Costa Rica). In this case, the tree was definitely not *I. marginata* (I. Chacon, pers. comm.). A summary by Ackery (1988) indicates that host plants of 11 *Morpho* species include various genera of the Fabaceae. The report of Brazilian *M. rhetenor* (Cramer, 1777) feeding on *Macrolobium* (Fabaceae) by Ackery (1988) is important in the context of a potential sister species relationship between *M. cypris* and *M. rhetenor* (Le Moult and Real, 1962; DeVries et al., 1985). The trend for *Morpho* to use Fabaceae broadly, and the relationship of *cypris* and *rhetenor* suggest that both species may use *Inga* and *Macrolobium* as hosts, and that their diet will eventually include more members of the Fabaceae than is currently known. With respect to conservation biology this may be good news, because remnant patches of forest are likely to sustain a variety of suitable host plant species for these butterflies. On the other hand, all of our observations on *M. cypris* in Costa Rica and Panama suggest that adult territorial and courtship interactions occur only in or adjacent to sizable tracts of intact forest. Thus, in the face of increasing tropical deforestation, population levels of *M. cypris* may become critically low even in the presence of abundant larval host plants.

Butterflies live, interact, and die within dynamic biological systems, and as such they cannot be protected or conserved as objects or things (Sibatani, 1992). More than 140 years after *M. cypris* received its formal scientific name, our understanding of its early stage biology is confined to the information presented here—a sobering commentary on one of the most spectacular of all butterflies, and on our knowledge of tropical systems in general. Current devastation of these tropical systems is widespread. It is our hope that this paper will encourage further study of the biology and conservation of *M. cypris* butterflies and its tropical forest habitats. If such studies are not undertaken and published, then this and other papers will serve as an elegy.

ACKNOWLEDGMENTS

We wish to thank the Servicios Parques Nacionales de Costa Rica and the Museo Nacional de Costa Rica for providing field support for this study. Many thanks to the staff of the Dept. of Entomology, American Museum of Natural History for facilitating the publication of this study. The comments of N. Greig, J. Shinn, C. Snyder, J. Miller, and E. Quinter greatly improved the manuscript. A special thanks to J. Miller and F. Stehr for references and advice relating to caterpillar morphology. DeVries gratefully acknowledges the help of R. Canet, P. Chai, I. Chacon, N. Greig, and C. D. Thomas for assistance caring for early stages. DeVries wishes to express gratitude to the MacArthur Foundation for supporting all his recent research efforts. This study is dedicated to the late Miles Davis, Stan Getz and Dizzy Gillespie.

LITERATURE CITED

Ackery, P. R. 1988. Host plants and classification: a review of nymphalid butterflies. Biol. J. Linn. Soc. 33:95–203.

Bates, H. W. 1864. The naturalist on the river Amazon. John Murray, London.

Belt, T. 1874. The naturalist in Nicaragua. John Murray, London.

Bourgone, J. 1951. Ordre de Lepidopteres. Pages 174–448. *in:* P. Grasse (ed.), Traite de zoologie, anatomie, systematique, biologie. Tome X, Insectes (Insectes superieurs). Fasc. 1, Neuropteroides, Mecopteroides, Hymenopteroides. Masson, Paris.

Chai, P. 1990. Relationships between visual characteristics of rainforest butterflies and responses of a specialized insectivorous bird. Pages 31–60 *in:* M. Wickstein (ed.), Adaptive Coloration in Invertebrates. Texas A & M University, College Station.

D'Abrera, B. 1984. Butterflies of the Neotropical Region. part II. Danaidae, Ithomiidae, Heliconidae & Morphidae. Hill House, Victoria.

DeVries, P. J. 1987. The Butterflies of Costa Rica. Princeton University Press, Princeton.

DeVries, P. J., I. J. Kitching and R. I. Vane-Wright. 1985. The systematic position of *Antirrhea* & *Caerois*, with comments on the higher classification of the Nymphalidae. Syst. Ent. 10:11–32.

Forbes, W. T. M. 1948. Lepidoptera of New York and neighboring states. Part 2. Notodontidae. Cornell Agric. Exp. Stat. Mem. 329:203–207.

Kearby, W. H. 1975. Variable oakleaf caterpillar larvae secrete formic acid that causes skin lesions (Lepidoptera: Notodontidae). J. Kansas Ent. Soc. 48:280–282.

Le Moult, E. and R. Real. 1962. Les Morpho d'Amerique de Sud et Centrale. Novitates Ent. (supplement):1–296.

Miller, J. S. 1991. Cladistics and classification of the Notodontidae (Lepidoptera: Noctuoidea) based on larval and adult morphology. Bull. Am. Mus. 204:1–230.

Otero, L. S. 1966. Biologie de sept Lepidopteres Bresiliens du genre *Morpho* Fabricius, 1807. Ph.D. thesis, University of Paris.

Peterson, A. 1962. Larvae of insects, part 1: Lepidoptera and plant infesting Hymenoptera. Edwards Bros., Columbus, Ohio.

Sibatani, A. 1992. Decline and conservation of butterflies in Japan. J. Res. Lep. 29:305–315.

Stehr, F. W. 1987. Order Lepidoptera. Pages 288–305 *in:* F. W. Stehr (ed.), Immature Insects. Kendall/Hunt, Iowa.

Young, A. 1982. Notes on the natural history of *Morpho granadensis polybaptus* Butler (Lepidoptera: Nymphalidae: Morphinae), and its relation to that of *Morpho peleides limpida* Butler. J. New York Ent. Soc. 90:35–54.

Young, A. M. and A. Muyshondt. 1972. Biology of *Morpho polyphemus* (Lepidoptera: Morphidae) in El Salvador. J. New York Ent. Soc. 80:18–42.

Received 29 January 1993; accepted 1 June 1993.